Journal of Comparative Psychology
2009, Vol. 123, No. 3, 275–279

© 2009 American Psychological Association
0735-7036/09/$12.00 DOI: 10.1037/a0016220

Spatial Memory Recall in the Giant Panda (*Ailuropoda melanoleuca*)

Bonnie M. Perdue
Zoo Atlanta and Georgia Institute of Technology

Rebecca J. Snyder and Jason Pratte
Zoo Atlanta

M. Jackson Marr and Terry L. Maple
Georgia Institute of Technology

The current study tested spatial memory recall in 1 male and 1 female giant panda (*Ailuropoda melanoleuca*). The task required subjects to make a delayed response to a previously lighted location, with varying lengths of delay between the observation phase and the test phase. The male subject reached criterion at 2-, 3-, 4-, 5-, 6-, and 10-s delays. The female subject reached criterion at 2-, 3-, 4-, 5-, 6-, 10-, and 15-s delays. The results support the hypothesis that giant pandas demonstrate significant working memory for spatial location in the absence of external cues, which may be an important mechanism for survival in the wild.

Keywords: giant panda, spatial memory, working memory, recall

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

The giant panda (*Ailuropoda melanoleuca*) has stimulated a great deal of research in zoological institutions because of its unique biological characteristics, difficulties in captive breeding, and threats to its survival as a species (Lindburg & Baragona, 2004). Survival in the wild depends on an individual's ability to initially find and subsequently remember the location of resources such as food, potential mates, and threats, such as predators. However, only one study has investigated spatial memory in the giant panda (Tarou, 2003; Tarou, Snyder, & Maple, 2004), and some potentially confounding variables remain. The purpose of the current study was to focus on spatial working memory in the giant panda and to clarify and extend this previous work.

The natural history of giant pandas suggests the potential for spatial memory. Giant pandas show preferences for topography of feeding sites as well as distinct seasonal variation in the types of bamboo consumed, parts of bamboo consumed (leaves or stem), and age of plants consumed (Reid & Jinchu, 1991; Schaller, Jinchu, Wenshi, & Jing, 1985). Remembering the location of patches throughout the year would aid giant pandas in locating preferred food. Another driving force in the evolution of spatial memory may be that it improves reproductive success. Giant pandas mate with multiple partners during the breeding season (Schaller et al., 1985), and spatial memory could help an individual locate mates, communal scent marking areas, and birthing dens.

Bonnie Perdue, Zoo Atlanta, Atlanta, GA; School of Psychology, Georgia Institute of Technology. Rebecca Snyder and Jason Pratte, Zoo Atlanta, Atlanta, GA. M. Jackson Marr and Terry L. Maple, School of Psychology, Georgia Institute of Technology.

This research was supported in part by the Bailey Fund and the Smithgall Watts endowment. This project would not have been possible without the support and assistance of the Zoo Atlanta giant panda department. We are also grateful to Kenn Harwood and Daryl Hood for constructing the apparatus.

Correspondence concerning this article should be addressed to Bonnie Perdue, School of Psychology, Georgia Institute of Technology, Atlanta, GA 30332. E-mail: bonnie.perdue@gatech.edu

Tarou (2003) tested giant panda spatial memory with a naturalistic foraging task, an adaptation of the radial arm maze. Working memory for events in a specific session and reference memory for unchanging characteristics of the task (Shettleworth, 1998) were tested. In the exploratory phase, food items were placed inside eight feeders mounted around the subject's enclosure, and the pattern of foraging was recorded. In this type of task, the behavior of avoiding revisits to depleted feeders is often considered evidence of working memory. Tarou found a significant decrease in the number of revisits to depleted feeders over the course of this task. However, subjects also developed a preference for a direction of travel and starting feeder position, which may account for the decrease in revisits to depleted feeders. In other words, the avoidance of depleted feeders may simply reflect individual response patterns rather than the subject remembering which locations had been visited. Additional research is necessary to clarify whether giant pandas demonstrate significant spatial working memory.

The second phase of the study included a spatial and reversal task to test reference memory for spatial location (Tarou, 2003). In the spatial task, the same four feeders were baited for each session. Five subjects effectively used spatial cues to locate food within 30 sessions. To determine whether olfactory cues were being used to locate the baited feeders, a reversal task was included in which the opposite four feeders were baited with food. Subjects that had initially learned the spatial task visited the originally baited sites even though they no longer contained food. This disturbance in performance suggests that the subjects were not using olfactory cues to locate the baited feeders. However, locations were directly baited with food in this study, and it is tenable that olfactory cues influenced foraging behavior.

To test working memory for location in the giant panda, the current study required a delayed response to a previously lighted stimulus (Hunter, 1913; Medin, 1969) using a 2×3 light grid. A light was used to indicate a "baited" site, rather than actually baiting the site with food reinforcement, removing the presence of olfactory cues. Because the light was not re-presented prior to the

response, this task contained aspects of a recall task and required the subject to generate the target information at the time of the response (Brown, 1976). The design of the current apparatus also prevented the subject from following a rule of thumb, such as walking in a clockwise circle and visiting adjacent locations. Thus, we can distinguish spatial working memory from olfactory cues or response patterns. We hypothesized that subjects would successfully perform the task of selecting the previously lighted location with the 2-s delay condition and that performance (% correct responses) would decrease as the delay increased.

Method

Subjects

One male (born September 9, 1997) and one female (born August 25, 1997) adult giant panda (*Ailuropoda melanoleuca*) were tested for this study. Subjects were born at the Chengdu Research Base for Giant Panda Breeding and transported to Zoo Atlanta in 1999. Positive reinforcement training is used everyday with these subjects to facilitate husbandry and veterinary procedures, and they have participated in previous cognitive research, including one study of spatial memory (Tarou, 2003). The study was conducted in the indoor holding enclosure before the animals went on exhibit (0800–0830).

Apparatus

A wooden structure (50.8 cm × 76.2 cm × 15.2 cm) was divided into a grid pattern, forming six squares (18 cm × 18 cm). Each square contained a light source (7-W bulb) that could be operated and controlled independently with a rheostat. Full (37.2 candela per meter squared [cd/m^2]), medium (6.4 cd/m^2), and no light brightness levels were specified on the dial. The apparatus was attached to the mesh of the subject's enclosure on the experimenter's side so that the Plexiglas grid faced the subject. A piece of PVC pipe extended from the center of each bait site approximately 30 mm into the enclosure to serve as a button. Subjects were trained to push the buttons, which completed a circuit and resulted in the illumination of small light (only visible on the experimenter side), allowing the experimenter to monitor responses remotely. A target stick could be inserted through the center of the apparatus approximately 46 cm into the subject's enclosure, and could be shifted left or right (25.5 cm) to disrupt eye or postural contact during the delay.

Procedure

The male subject was trained and tested from August 2006 to April 2007, and the female was trained and tested from April 2007 to June 2008. Sessions occurred approximately 3 times per week and lasted 10 to 15 min. Subjects were trained to use the apparatus using a positive reinforcement technique in which an auditory stimulus (whistle) was paired with food delivery. Food items included small pieces of banana, apple, pear, sweet potato, and leaf-eater biscuit (approximately 100 g) and were delivered to the subject through the mesh of the enclosure.

Initial training was conducted on a two-square prototype apparatus. Responses (i.e., button pushes) to the lighted location resulted in reinforcement and the cue "light" was introduced. After the subject responded correctly to 10 of 15 trials when the apparatus was mounted in both the vertical and horizontal orientations, this behavior was transferred to the six-square apparatus. After the behavior of pushing a lighted square when given the command "light" was established (10 of 15 trials) on the six-square apparatus, the next phase of training began.

Using the target stick, a behavior chain was trained in which the subject targeted (i.e., touch nose to end of stick and remain stationary) in the center position (facing the apparatus), targeted a side position (randomly predetermined), and targeted the center position again. Then the target stick was withdrawn and the cue "light" was given. This behavior chain of repositioning the head and body was trained to prevent the subject from maintaining eye contact or postural contact with the light stimulus during later stages of testing.

There were two experimenters present for all training and testing sessions. Experimenter 1 stood behind the apparatus and cued the targeting behavior chain and delivered food for correct responses. Experimenter 1 was blind to the correct location on every trial. Experimenter 2 sat behind Experimenter 1 and the apparatus and controlled the lights via a remote dial. Experimenter 2 was responsible for turning the lights on and off, starting the timer, and providing auditory reinforcement for correct responses. There were 15 trials per session, and the correct locations were pseudorandomly determined for each session using a computer-generated sequence.

After the "light" behavior and the chain of target behaviors were established, a brightness-fading procedure was started. The first center target was followed by the auditory signal and one of the lights was turned on. Then, the subject targeted the side position, and the saliency of the light was changed from full brightness to medium brightness. The subject targeted in the center again, the target stick was withdrawn, and the command "light" was given. The subject had to approach the apparatus and push the button for the correct location (which was at medium brightness). Correct responses resulted in the auditory signal followed by food reinforcement.

After subjects responded to 10 of 15 trials correctly, the brightness-fading technique was combined with a time-fading procedure. The same procedure was followed, except that the experimenter slowly faded the light as the subject approached the apparatus. At first, the light was not fully extinguished until the subject pushed the button. As the training progressed, the light was dimmed more rapidly and was fully extinguished as the animal neared the apparatus, then as the subject began to approach the apparatus, and then as the animal was prompted by the withdrawal of the target stick and the command light. Finally, the light was turned off completely as the subject targeted to the side position. After the subject reached criterion for this procedure (8 of 15 correct), the delayed response phase of testing began.

A trial began when the subject targeted in the center position, resulting in the auditory signal and the illumination of the correct location for 3 s. Then the subject targeted to a side position, during which the light was extinguished and a 2-s delay began. Then the subject targeted back to the center and remained in this position until a stimulus (vibrating timer) cued Experimenter 1 that the delay had elapsed. At this point, the target stick was withdrawn and the subject was prompted by the command "light" to approach the apparatus and push the previously lighted square. A correct

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

response resulted in the auditory stimulus followed by the delivery of food. The intertrial interval was approximately 10 s and concluded when the subject finished consuming the food item and repositioned in front of the apparatus. An incorrect response resulted in the auditory stimulus "NO," followed by an approximately 5-s intertrial interval during which no food or attention was provided to the subject. Subjects remained in this phase of testing until performance reached a criterion value of 8 of 15 correct responses for 2 consecutive days (see *Data Analysis*).

Phase 2 explored how performance changed with increasing delay. An abrupt shift to longer delays was expected to alter and disturb performance; therefore, delay durations were incrementally increased. Furthermore, to monitor for confounding influences, 2-s delay trials were included in all sessions. If the performance on the 2-s delay trials in a session fell below chance, it could not be expected that the performance on the longer delays would accurately reflect the subjects' ability to respond following a longer delay. Rather, it may reflect a subject's lack of motivation, a high level of distraction, or perseverative responding during that session. Essentially, the 2-s delay served as the baseline for performance. If performance at the 2-s delay remained stable, responses to the longer delays were considered an accurate reflection of ability.

Phase 2 sessions included eight 3-s trials and seven 2-s trials. Subjects were tested for 32 trials (four sessions) to determine whether they could respond accurately at a 3-s delay. Testing was considered complete for the 3-s delay at any point at which criterion (see *Data Analysis*) was met. For any subject that reached criterion, a 4-s delay was added. There were eight 4-s delays and seven 2-s delays. The procedure proceeded as described above. For any subject that reached criterion for a 4-s delay, the same procedure was repeated for the 5-s delay, and so forth. The delay times used were 3, 4, 5, 6, 10, 15, and 20 s. Testing was considered complete for a subject when it failed to respond correctly to the longer delay for four sessions (32 trials) while maintaining accurate performance on the 2-s delay.

Data Analysis

To limit the possibility that acquisition of the task was because of chance, we used a binomial distribution to determine the criterion performance values. It was assumed that trials were independent and the outcome of each trial was discrete (correct or incorrect). Because there were six response options, the probability of randomly responding correctly on a trial was 16.7%. As modeled by a binomial distribution, 8 of 15 correct responses were significantly different than chance ($p = .001$). For Phase 2 of testing, criterion values of 4 of 8 correct responses ($p = .026$) on the longer delays and 4 of 7 correct responses ($p = .016$) on the baseline 2-s delays were significantly different than chance.

A post hoc analysis of errors was conducted to determine whether incorrect responses were influenced by the location information presented on the previous trial (i.e., proactive interference) or by information presented on the current trial (i.e., adjacency). If subjects were responding randomly when incorrect, the probability of responding to the previously presented location was 1 of 5 (20%). A binomial distribution was used to determine whether the actual number of responses to the previously presented location differed from chance. Next, the locations of incorrect responses were scored as "adjacent" (i.e., two locations share an edge) or "nonadjacent" to the correct location. The probability of randomly responding to an adjacent location was 2 of 5 (40%) for corner locations and 3 of 5 (60%) for noncorner locations. For each subject, we used a binomial distribution for each location to determine whether incorrect responses were more likely to be to an adjacent location than expected by chance.

Results

Given the small sample size, the results are limited to the spatial memory of the subjects in the study, and no inferences regarding the population are made. Both subjects reached criterion (8 of 15) for the 2-s delay. In Phase 2 of testing, both subjects reached criterion (4 of 8) for 3-, 4-, 5-, 6-, and 10-s delays, and the female also passed criterion for the 15-s delay. The male subject reached criterion in one session for the 10-s delay, two sessions for the 2-, 5-, and 6-s delays, three sessions for the 3- and 4-s delays, and did not reach criterion in four sessions for the 15-s delay (see Table 1). The female subject reached criterion in one session for the 4-s delay, two sessions for the 2-, 3-, 5-, 6-, 10-, and 15-s delays, and did not reach criterion in four sessions for the 20-s delay (see Table 1). Performance on the first session that a longer delay was

Table 1
Number of Correct Responses on First and Last Sessions and Number of Sessions Needed to Reach Criterion for Each Delay

		Male			Female		
Delay	Criterion	First session	Last session	Sessions to criterion	First session	Last session	Sessions to criterion
2 s	8/15	8	9	2	8	9	2
3 s	4/8	2	5	3	3	4	2
4 s	4/8	3	4	3	4	4	1
5 s	4/8	1	5	2	1	4	2
6 s	4/8	3	5	2	2	4	2
10 s	4/8	5	5	1	3	4	2
15 s	4/8	2	3[a]	—	3	4	2
20 s	4/8				2	2[a]	—

Note. Criterion values are significantly different than chance as modeled by a binomial distribution: 8 of 15 for 2-s delay ($p = .001$) and 4 of 8 for longer delays ($p = .026$). Subjects were given four sessions to reach criterion performance for each delay.
[a] Subject did not reach criterion within four sessions.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

introduced varied across individuals and delays, as shown in Table 1.

When incorrect, subjects were significantly *less* likely than chance (20%) to respond to the previously correct location (female: 18 of 145 [12.4%], $p = .005$; male: 17 of 127 [13.4%], $p = .015$). Subjects responded to an adjacent location more often than expected by chance, significantly more for three of six locations (see Table 2).

Discussion

The results support the hypothesis that giant pandas demonstrate working memory for spatial information in the absence of external cues. The current design eliminated the possibility that subjects were responding to olfactory cues because the locations were indirectly baited with light, rather than food. The results also support the hypothesis that memory performance should decline as the delay increases, and suggest that giant pandas reach a threshold after an approximately 10- to 15-s delay in which remembering spatial information becomes increasingly difficult.

In some spatial memory studies, information from previous trials interferes with performance (i.e., proactive interference; Lewis & Kamil, 2006). However, our results indicate that responses on incorrect trials were not influenced by the information presented in the previous trial. Instead, we found that subjects were more likely to respond to adjacent locations when incorrect, suggesting that subjects were able to remember general information (e.g., left), but more specific information (e.g., top left) was not retained across the delay.

Factors such as motivation, distraction, and perseveration may also affect performance on delayed response memory tasks. Sessions were conducted in the morning as an attempt to ensure reasonable food motivation and to minimize distraction. Two-second delays were included in all sessions with longer delay times. The subject would not be considered to fail a longer delay if performance on the 2-s delay fell below criterion for all testing sessions. This did not happen for either subject, and performance on the shortest delay remained above criterion when the performance on longer delays fell below chance. Another issue in spatial memory tasks is the animal using its own body as a cue during the delay (Shettleworth, 1998). To prevent this possibility, the current study required subjects to turn their heads and bodies away from the apparatus as the light was being extinguished, and the apparatus and procedure were designed to prevent experimenter cueing.

An important outcome of the current study is the development of a task capable of testing recall memory. The majority of memory studies in nonhuman species have been conducted using recognition tasks (Eacott & Easton, 2007); more research is needed addressing recall. Although the current task may not be considered pure recall, it assesses a critical aspect of recall memory. Specifically, the subject is required to generate the target information without explicit environmental cues (Brown, 1976). This experimental design could be used to test recall memory in many species that are not suitable candidates for computerized testing.

This research significantly adds to our understanding of giant panda spatial memory. Foraging and reproductive efforts may have benefited from remembering location information and resulted in spatial memory in the giant panda. Previous research has found that giant pandas demonstrate spatial reference memory for food locations (Tarou, 2003) and can remember discriminations of face-like patterns for up to a year (Dungl, Schratter, & Hubel, 2008). The current study provides a controlled test of working spatial memory recall. Accordingly, the retention intervals were shorter than those found in a more naturalistic task taking place in a three-dimensional, salient environment or in a task using ecologically relevant stimuli. The current study provides clear evidence of working memory recall for spatial location in the giant panda. A larger sample of giant pandas should be tested to progress the currently limited knowledge of cognition in this species.

Table 2
Expected and Actual Percentage of Incorrect Responses to Adjacent Locations

		Male			Female		
Location	Expected % (adj. locations)	No. errors	Actual %	*p*	No. errors	Actual %	*p*
1	40.0 (2, 4)	11	72.7*	.02	27	70.4*	.001
2	60.0 (1, 3, 5)	32	81.3*	.006	13	69.2	.18
3	40.0 (2, 6)	13	61.5	.06	22	63.6*	.01
4	40.0 (1, 5)	21	61.9*	.02	31	51.6	.06
5	60.0 (2, 4, 6)	32	59.4	.14	26	61.5	.15
6	40.0 (3, 5)	18	50.0	.12	26	69.2*	.00

Note. Locations were numbered as shown in grid below and "adjacent" was scored for locations that share one edge.

1	2	3
4	5	6

* $p < .05$.

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

References

Brown, J. (1976). *Recall and recognition.* New York: Wiley Interscience.

Dungl, E., Schratter, D., & Huber, L. (2008). Discrimination of face-like patterns in the giant panda (*Ailuropoda melanoleuca*). *Journal of Comparative Psychology, 122,* 335–343.

Eacott, M. J., & Easton, A. (2007). On familiarity and recall of events in rats. *Hippocampus, 17,* 890–897.

Hunter, W. S. (1913). The delayed reaction in animals and children. *Animal Behaviour Monographs, 2,* 1–86.

Lewis, J. L., & Kamil, A. C. (2006). Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana. Journal of Experimental Psychology, Animal Behavior Processes, 32,* 407–418.

Lindburg, D., & Baragona, K. (2004). Introduction: A new dawning for giant pandas? In D. Lindburg & K. Baragona (Eds.), *Giant pandas: Biology and conservation* (pp. 1–6). Berkeley: University of California Press.

Medin, D. L. (1969). Form perception and pattern reproduction by monkeys. *Journal of Comparative and Physiological Psychology, 68,* 412–419.

Reid, D. G., & Jinchu, H. (1991). Giant panda selection between *Bashania fangiana* bamboo habitats in Wolong reserve, Sichuan, China. *Journal of Applied Ecology, 28,* 228–243.

Schaller, G. B., Jinchu, H., Wenshi, P., & Jing, Z. (1985). *The giant pandas of Wolong.* Chicago: University of Chicago Press.

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.

Tarou, L. R. (2003). *An examination of the role of associative learning and spatial memory in foraging in two species of bear (family: Ursidae*). Unpublished doctoral dissertation, Georgia Institute of Technology, Atlanta.

Tarou, L. R., Snyder, R. J., & Maple, T. L. (2004). Spatial memory in the giant panda. In D. Lindburg & K. Baragona (Eds.), *Giant pandas: Biology and conservation* (pp. 101–105). Berkeley: University of California Press.

Received November 12, 2008
Revision received March 5, 2009
Accepted April 12, 2009 ■

This document is copyrighted by the American Psychological Association or one of its allied publishers.
This article is intended solely for the personal use of the individual user and is not to be disseminated broadly.

Call for Nominations

The Publications and Communications (P&C) Board of the American Psychological Association has opened nominations for the editorships of **Experimental and Clinical Psychopharmacology, Journal of Abnormal Psychology, Journal of Comparative Psychology, Journal of Counseling Psychology, Journal of Experimental Psychology: Human Perception and Performance, Journal of Personality and Social Psychology: Attitudes and Social Cognition, PsycCRITIQUES, and Rehabilitation Psychology** for the years 2012–2017. Nancy K. Mello, PhD, David Watson, PhD, Gordon M. Burghardt, PhD, Brent S. Mallinckrodt, PhD, Glyn W. Humphreys, PhD, Charles M. Judd, PhD, Danny Wedding, PhD, and Timothy R. Elliott, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2011 to prepare for issues published in 2012. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- **Experimental and Clinical Psychopharmacology,** William Howell, PhD
- **Journal of Abnormal Psychology,** Norman Abeles, PhD
- **Journal of Comparative Psychology,** John Disterhoft, PhD
- **Journal of Counseling Psychology,** Neil Schmitt, PhD
- **Journal of Experimental Psychology: Human Perception and Performance,** Leah Light, PhD
- **Journal of Personality and Social Psychology: Attitudes and Social Cognition,** Jennifer Crocker, PhD
- **PsycCRITIQUES,** Valerie Reyna, PhD
- **Rehabilitation Psychology,** Bob Frank, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to http://editorquest.apa.org. On the Home menu on the left, find "Guests." Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Emnet Tesfaye, P&C Board Search Liaison, at emnet@apa.org.

Deadline for accepting nominations is January 10, 2010, when reviews will begin.